



Water column use by reef fishes of different color patterns

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Color in animals responds to selective pressures and mediates the relationship between organism and environment. Reef fishes have the amplest variety of pigment cell types. This color patterns' variety may function as camouflage and be related to spatial use. We tested the hypothesis that the coloration of reef fish relates to water column stratum occupation. We predicted that sedentary animals connected to the background take advantage of background matching or disruptive patterns; more mobile demersal species apply disruptive coloration or motion-dazzle; and that pelagic species tend to have silvery bodies. We classified color patterns and categorized the water column stratum use for the Brazilian reef fishes in FishBase. Our analyses confirmed that irregular contrasting contour breaks, suggestive of disruptive coloration, occurs in benthic species and that silvering color was more prevalent in the pelagic stratum. Our raw data suggested a higher frequency of contrasting regular stripes, typical of motion-dazzle, in demersal species. However, the considerable uncertainty around estimates did not confirm this pattern. Reef fishes coloration is correlated to occupation of different strata in the water column. This can be interpreted as fishes being adapted to these habitats and partially explaining the richness of color patterns among them.

Keywords: Background matching, Camouflage, Disruptive coloration, Habitat use, Predator-prey interaction.

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A cor nos animais responde a pressões seletivas e media a relação entre organismo e ambiente. Peixes recifais têm a maior variedade de tipos de células de pigmento. Essa variedade de padrões de coloração pode funcionar como camuflagem e estar relacionada ao uso espacial. Nós testamos a hipótese de que a coloração dos peixes recifais está relacionada à ocupação do estrato da coluna d'água. Previmos que animais sedentários conectados ao fundo aproveitam a semelhança ao fundo ou padrões disruptivos; espécies demersais mais móveis aplicam coloração disruptiva ou deslumbramento de movimento; e que espécies pelágicas tendem a apresentar corpos prateados. Classificamos os padrões de coloração e categorizamos o uso do estrato da coluna d'água para os peixes recifais brasileiros no FishBase. Nossas análises confirmaram que quebras de contorno irregulares, sugerindo coloração disruptiva, ocorrem em espécies bentônicas e que a cor prateada prevaleceu no estrato pelágico. Nossos dados brutos sugeriram uma maior frequência de listras contrastantes, típicas do deslumbramento de movimento, em espécies demersais. Mas a considerável incerteza dessas estimativas não confirmou esse padrão. A coloração dos peixes recifais está correlacionada com a ocupação de diferentes estratos da coluna d'água. Isso pode ser interpretado como peixes sendo adaptados a estes habitats, explicando em parte a riqueza de padrões de coloração entre eles.

Palavras-chave: Camuflagem, Coloração disruptiva, Interação predador-presa, Semelhança ao fundo, Uso do habitat.

INTRODUCTION

Perceived colors depend on the light absorption by skin pigments, light scattering, or by a combination of both (Shawkey *et al.*, 2009; Cronin *et al.*, 2014). The color of animals responds to selective pressures and mediates the relationship of an organism with the environment in different ways, functioning as social signaling, thermoregulation, UV-protection, mate attraction, intrasexual competition, and camouflage (Cuthill *et al.*, 2017; Marshall, 2000).

The risk of death by predation is one of the main determinants of fitness (Carr, Hixon, 1995). Predation as a selective pressure affects body shape and behavior of organisms (Van Der Laan, Hogeweg, 1995), such as increased physical and chemical defenses by prey and reduced body sizes (Hammerschlag *et al.*, 2018). In addition, prey may escape predation by going unnoticed by predators via camouflage: the set of strategies that reduce the chance of prey being detected or recognized by predators (Stevens, Merilaita, 2008).

Visual camouflage can be divided into several strategies, including background matching, silvery bodies, disruptive patterns, and motion-dazzle (Stevens, Merilaita, 2008). Background matching occurs when the color, brightness, or pattern of the individual resemble the properties of the environment, therefore decreasing the probability of detection by a predator (Merilaita *et al.*, 1999). For fishes that live farther from the bottom and are highly mobile, a symmetrical cylindrical or fusiform silvery body in an underwater light field reflects a region of the water column that corresponds to what is behind the mirror (Ruxton *et al.*, 2004; Johnsen, 2014), making it difficult to detect the animal. Thus, silvering is a case analogous to background matching with

the fish matching by reflection the ocean behind it. Either via silvering or coloring, background matching has an implicit cost of restricting an individual to the set of substrates to which their coloration provides effective camouflage (Tyrie *et al.*, 2015), at least if the animal has restricted ability to change colors, as most reef fishes.

An alternative to the dependence of the substrate that background matching demands would be disruptive coloration: a color pattern that makes it difficult to detect the animal by disguising its contour, such as the marine isopods *Idotea balthica* (Pallas, 1772) (Merilaita, 1998). Disruptive patterns obscure the shape of the animal, mixing it partially in the background, hindering the detection of the contour of its body (Cuthill *et al.*, 2005). In addition to disruptive coloration, stripes may also reduce the risk of predation via motion-dazzle. The combination of high-contrast repetitive stripes makes estimates of speed and trajectory of prey less precise (Hogan *et al.*, 2016; Negro *et al.*, 2020). Similar to disruptive coloration, motion-dazzle may also allow animals to occupy a greater variety of habitats. For instance, striped individuals *Hippocampus reidi* Ginsburg, 1933 seahorses were found in a greater variety of micro-habitats than individuals with homogenous coloration (Duarte *et al.*, 2019), and in *Alpheus* Fabricius, 1798 shrimps the evolution of a banded pattern was more frequent in microhabitat generalists than in microhabitat specialist species (Elias *et al.*, 2019). Therefore, for demersal mobile fishes a disruptive or motion-dazzle strategy may be more effective than background matching. The mobility and the greater distance from the substratum may cause the individual to be viewed at a greater variety of habitats than benthic species. However, a motion-dazzle pattern should not be typical in benthic more sedentary fishes because the regularity of the bands may make the fish more detectable than a background matching or disruptive strategy (Stevens *et al.*, 2011).

Reef fishes are vertebrates with the widest variety of known pigment cell types (Schartl *et al.*, 2016), offering diverse color patterns, including dark or evident colors and a combination of stripes, spots, and bands (Salis *et al.*, 2019). Their color patterns may vary according to sex, ecology, and stage of development (Cortesi *et al.*, 2015). Reefs are heterogeneous habitats, full of predators (Mihalitsis, Bellwood, 2019) and are populated by a diversity of fish with different degrees of mobility, being a challenge for animals that camouflage themselves to avoid predation (Dorenbosch *et al.*, 2009). Up to 53% of the reef species are piscivores of greater or lesser voracity (Mihalitsis, Bellwood, 2019). Predation is one of the factors related to mortality and biological limitations in reefs. The species *Acanthochromis polyacanthus* (Bleeker, 1855), for example, grow larger in environments where there is no predation (Connell, 1998). In another study, relief of predation pressure caused by shark fishing resulted in morphological changes in reef fishes, such as caudal fins shape and relatively smaller eyes (Hammerschlag *et al.*, 2018). Those studies demonstrate the importance of predation in the ecomorphology of reef fishes. In addition, human impacts, such as mining in coral reefs and coral bleaching in response to climate change and the pH of seawater, can have a marked effect on the color of these environments and, consequently, on the survival of the species that inhabit coral reefs (Brown, 1997). This threatens one of the largest sources of biodiversity on the planet (Knowlton *et al.*, 2010).

Thus, the present work investigates habitat use by reef fishes of different color patterns. We seek to understand how reef fishes with varying degrees of mobility and positions in the water column avoid being detected by predators to better comprehend

the functioning of these rich environments. We hypothesized that the mobility and stratum of the water column influence the coloration. We predicted that sedentary animals that live close to the substrate take advantage of background matching or disruptive coloration, that more mobile demersal animals apply disruptive coloration or motion-dazzle, while highly mobile pelagic species tend to have silvery bodies.

MATERIAL AND METHODS

Our study evaluated the coloration and habitat use of Brazilian reef fishes, both Actinopterygii and Chondrichthyes, with data available on Fishbase (Froese, Pauly, 2019). This is a recognized database among ichthyologists. It was developed by the International Center for Living Aquatic Resources Management (ICLARM) together with the Food and Agriculture Organization of the United Nations (FAO), with support from the Commission of the European Communities (CEC) (Froese, 1991). The data relating to the records of different fish families are curated by a group specialist, giving considerable accuracy to the information presented there. With the data found in FishBase, we collected the following information: scientific name, popular name of the species, family, geographical distribution, and position in the water column it occupies (adults in non-reproductive period).

From the photographs of the species present on the platform, we determined the following aspects of their coloration (Fig. 1): the presence of a moderately homogenous non-silvering color pattern without large contrasting patches (typical of background matching), a relatively homogenous silvery body (typical of silvering), presence of highly contrasting regular stripes (*e.g.*, black and white stripes; typical of motion-dazzle strategy), and presence of contrasting contour breaks patches (typical of disruptive coloration). We also categorized the use of the water column stratum into benthic (species closely related to the bottom, remaining sheltered or propped on the substrate and with less mobility), pelagic (highly mobile species that live at half water or near the surface), and demersal (species that are functionally between benthic and pelagic, living associated to the substrate, but also with good mobility) (Friedman *et al.*, 2020). The photographs were categorized visually by one of us (FMG). Some species may present more than one type of coloration. For instance, the presence of stripes as well as contrasting patches typical of disruptive coloration. In those cases, we classified fishes by the coloration type more readily distinguished.

We analyzed the data in a Bayesian multinomial multilevel model. We present statistical estimates as the mode and credible intervals. In Bayesian analysis the credible intervals are the probability that the true value lies within the interval. In a pairwise comparison, when the 95% credible interval does not cross zero, there is a probability of at least 95% that the difference between estimates is not zero. The color category entered as the response variable (four levels: homogenous non-silvering, contrasting non-striped patches, contrasting stripes, and homogenous silvering) and the position in the water column as the predictor variable (three levels: benthic, demersal, and pelagic). We included the phylogenetic tree (phylogenetic distances) as a group-level factor (random effects) to model the phylogenetic dependence between fish species. We generated the phylogeny using data from the Open Tree of Life, with the *rotl* package (Michonneau

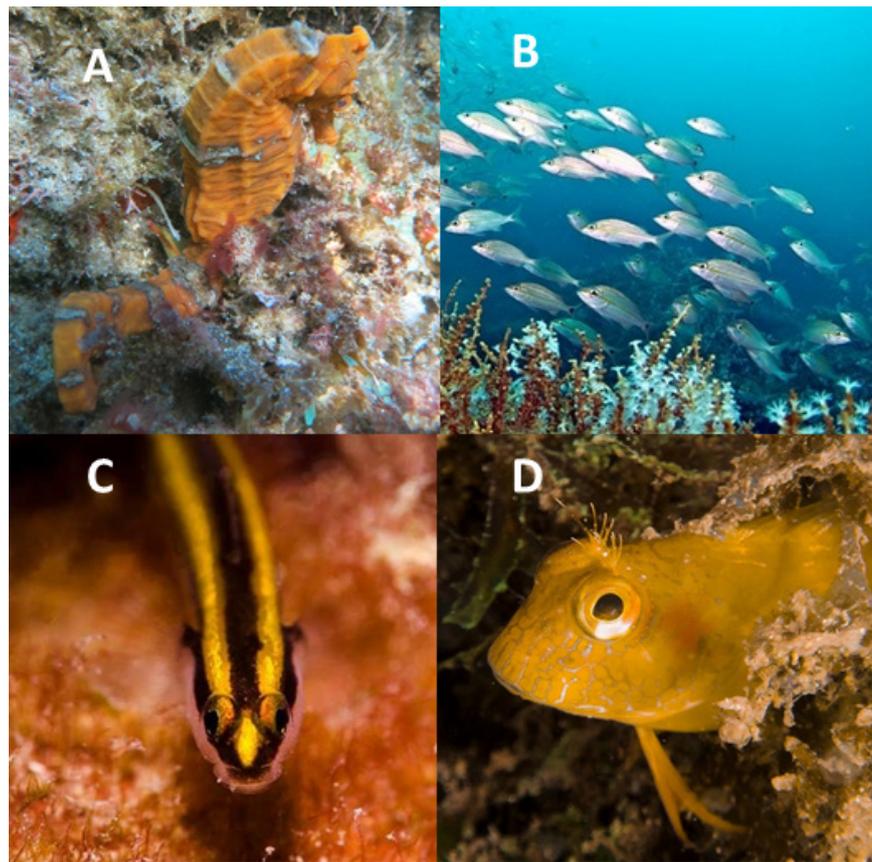


FIGURE 1 | Species exemplifying the color patterns used in this study. **A.** Large contrasting patterns typical of disruptive coloration in *Hippocampus reidi* (~ 13 cm of total length, TL); **B.** Silvery bodies in *Haemulon aurolineatum* Cuvier, 1830 (~ 18 cm TL); **C.** Contrasting stripes typical of motion-dazzle in *Elacatinus figaro* Sazima, Moura & Rosa, 1997 (~ 3 cm TL); **D.** Homogeneous coloration in adult female *Parablennius pilicornis* (Cuvier, 1829) (~ 6 cm TL). Photographs by Gualter Pedrini.

et al., 2016) of the software R version 4.0.2 (R Development Core Team, 2020). The branch lengths were estimated using the Grafen method (Grafen, 1989) in ape package (Paradis, Schliep, 2019) R version 4.0.2 (R Development Core Team, 2020).

We ran the Bayesian models using the package *brms* (Bürkner, 2017), which implements Bayesian models in *Stan* (Bürkner, 2018) in R version 4.0.2 (R Development Core Team, 2020). We set the default weakly informative priors (Tab. S1). We ran four independent chains for 30,000 iterations; 15,000 was a warm-up, in a total of 60,000 sampled iterations. We evaluated model fit by checking chain convergence, the presence of transitions with diverging errors, and visual checks of posterior predictive values.

RESULTS

We analyzed a total of 100 reef fish species (Fig. 2). Thirty-five were classified as benthic, 35 as demersal, and 30 as pelagic. We observed 30 homogeneous species, 31 with contrasting irregular patches, 25 with a silvery coloration, and 14 with contrasting

stripes. The data indicated that the benthic stratum is dominated by species with contrasting irregular patches, whereas the pelagic stratum is dominated by species with silvering coloration (Fig. 3). Striped colorations are predominantly found in demersal species (Fig. 3). Contrary to our hypothesis, the proportion of homogenous coloration is similar in benthic, demersal, and pelagic species (Fig. 3).

Our statistical analysis partially confirmed these trends (Fig. 4; Tab. S2). There was a decrease in the proportion of contrasting patches for demersal and pelagic species in comparison to benthic species; and an increase in the proportion of silvering for pelagic species in comparison to benthic and demersal species (Fig. 4); The data also

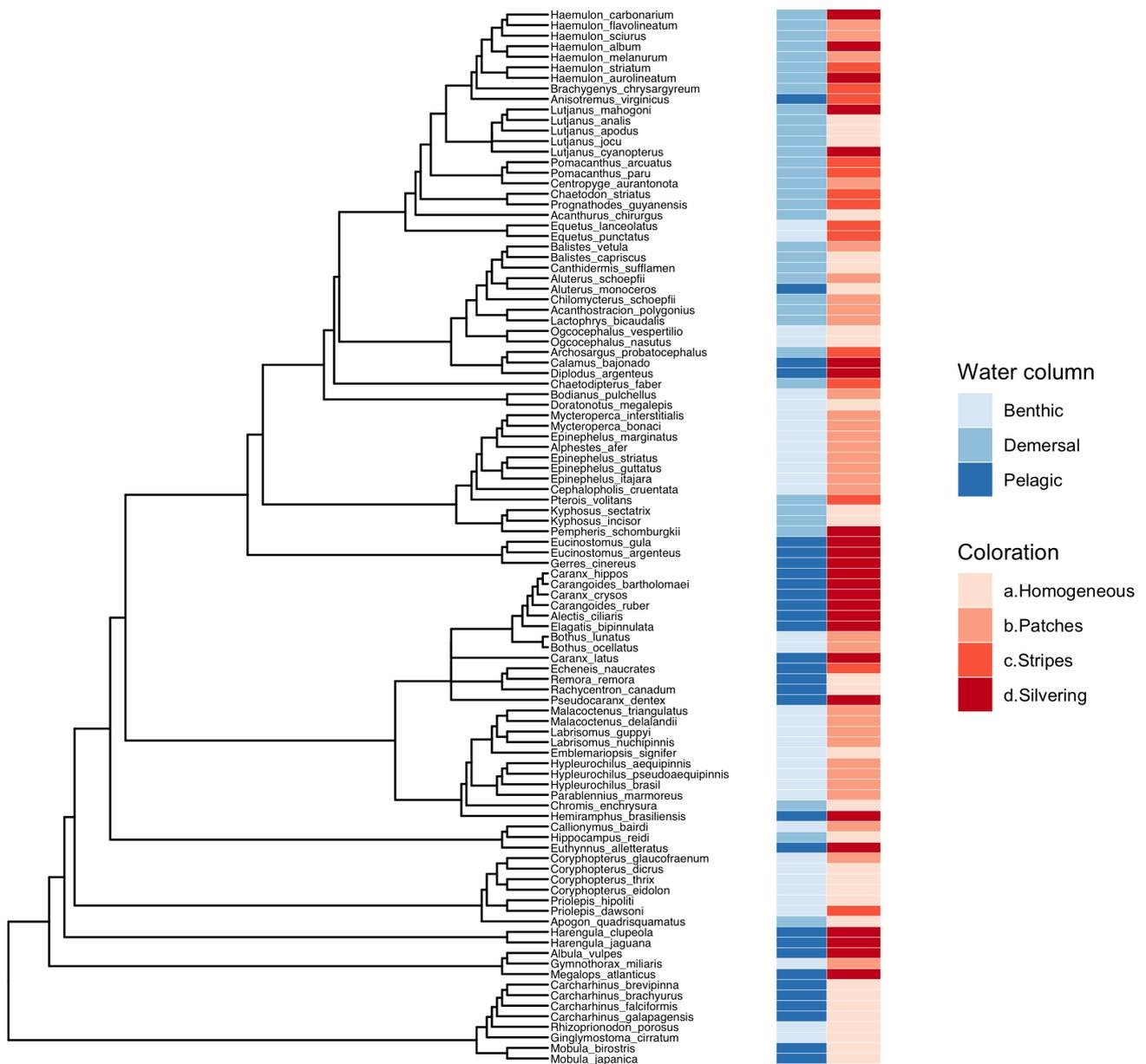


FIGURE 2 | Phylogeny of the 100 species used in this study generated from data in the Open Tree of Life. Branch lengths represent phylogenetic distance and were estimated by the Grafen's method. Color bars denote the water column use (blue shades) and coloration pattern (red shades) we attributed to them.

suggested an increase in the proportion of stripes for demersal species in comparison to benthic and pelagic species but uncertainty around statistical estimates did not confirm this pattern (Fig. 4). The analysis did not show any evident change in homogenous coloration between strata (Fig. 4).

DISCUSSION

Our results support the prediction that animals closely related to the reef bottom take advantage of contrasting irregular patches, while highly mobile pelagic species use to have silvering coloration. However, the statistical analysis did not confirm the predictions of a higher proportion of homogenous coloration in benthic species nor the higher proportion of stripes in demersal fishes.

We observed that fish species with contrasting non-regular patches, typical of disruptive coloration, were more present in the benthic stratum. Disruptive patterns are less background-dependent and may be more frequent in microhabitat generalist species. Nonetheless, disruptive coloration often blends with background matching, being more effective when it involves background-like spots along with disruptive patterns (Thayer, 1909; Poulton, 1940; Stobbe, Schaefer, 2008). When combined with low movement and proximity to the substrate, disruptive coloration and background matching may ensure protection against predators, and may also provide low detectability by prey, since there are many sit-and-wait benthic predators that camouflage efficiently against the substrate (*e.g.*, soles Tyrie *et al.*, 2015; Akkaynak *et al.*, 2017; and groupers Watson *et al.*, 2014).

Silvery species, such as *Carax bartholomaei* Cuvier, 1833, were more recurrent in the pelagic stratum. This result was already expected due to the non-availability of refuges and the habitat homogeneity in the pelagic stratum. Due to the refraction of light (Denton *et al.*, 1972), in mean waters of the oceans and deep lakes, silvery fishes have the advantage of being less visible, which decreases the detection of possible visual predators. Moreover, silvery fishes present other strategies to pass unnoticed by predators (McFall-Ngai, 1990). The advantage of silvering does not remain when seen directly from above or from below. In these cases, a way to decrease detection is to be flattened laterally (Ruxton *et al.*, 2004). Further, many pelagic species present countershading, another kind of background matching in which animals match their upper dark surface to the dark bottom of the sea, while they also match their light-colored lower surface to coincide with the solar lighting (Archer *et al.*, 1999; *e.g.*, *Carcharhinus brachyurus* (Günther, 1870)). Therefore, highly mobile pelagic fishes camouflage in such open and unprotected environment by confusing themselves with the ocean around them.

We observed striped coloration, typical of motion-dazzle, in mobile demersal and pelagic species, such as *Brachygenys chrysargyrea* (Günther, 1859) and *Prognathodes guyanensis* (Durand, 1960). This raw data agrees with our initial hypothesis that demersal animals apply motion-dazzle and disruptive coloration. The demersal stratum lies between the surface and bottom, so the fishes that inhabit this stratum are expected to be intermediate in swimming abilities and general coloration between pelagic and benthic fishes (Froese, Pauly, 2019). In addition to moving on several types of backgrounds, the distance demersal species maintain from the substrate causes

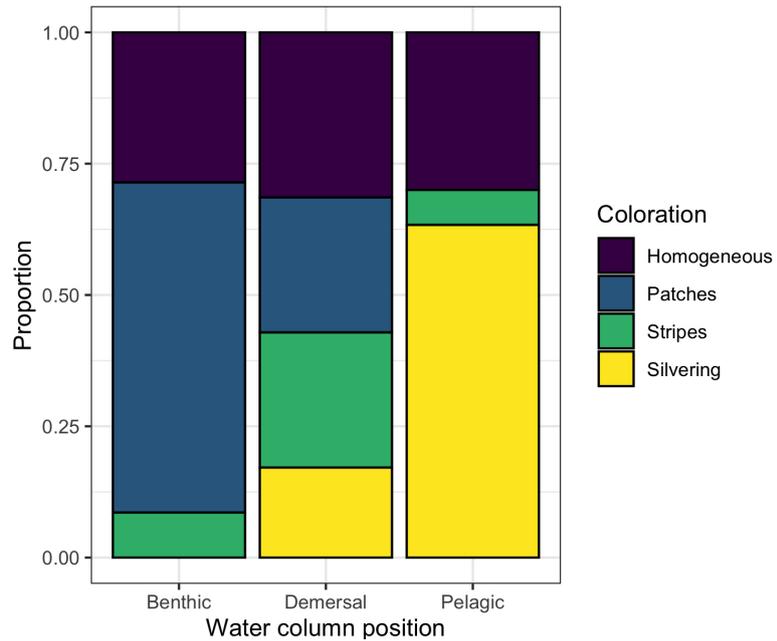


FIGURE 3 | Coloration of reef fish species by their position in the water column (benthic, $n = 35$; demersal, $n = 35$; pelagic, $n = 30$). Homogeneous refers to the presence of a moderately homogenous non-silvering color pattern without large contrasting patches (typical of background matching); patches refer to the presence of contrasting contour breaks patches (typical of disruptive coloration); stripes refer to the presence of highly contrasting regular stripes (*e.g.*, black and white stripes, typical of motion-dazzle strategy), and silvering to fishes with silvery homogenous body coloration.

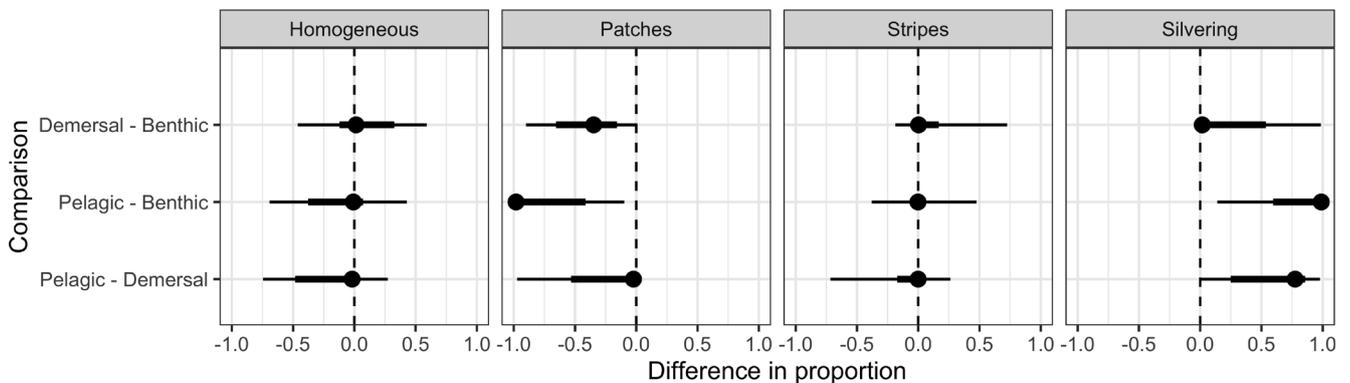


FIGURE 4 | Results of the Bayesian statistical analysis showing the difference in the proportion of coloration types between positions in the water column. Points denote the mode; thick and thin lines denote 67% and 95% credible intervals. Comparisons based on the expected values of the posterior predictive distribution. The analysis indicated that presence of contrasting contour breaks patches is more frequent in benthic than in demersal and pelagic species; and that silvering is more frequent in pelagic species than in demersal and benthic species.

predators at different depths to see demersal fishes against different backgrounds due to the parallax effect (Frost, 2010; Cuthill *et al.*, 2019). Therefore, we expected disruptive coloration and motion-dazzle to be more advantageous than background matching in demersal species (Duarte *et al.*, 2016). However, due to the large credible intervals

of the estimates, our statistical analysis did not confirm the trend we found in the raw data (Figs. 2–3).

Contrary to our prediction, fishes with homogeneous coloration were present in the three strata with similar frequencies (Figs. 2–3). We expected homogeneous colored fishes to represent background matching species, but this category included more diverse coloring, such as a body coloration free of a clear pattern but with visible moderately contrasting spots (e.g., *Emblemariopsis signifer* (Ginsburg, 1942) and *Coryphopterus dicrus* Böhlke & Robins, 1960) and stripes (e.g., *Acanthurus chirurgus* (Bloch, 1787)), or species with striking countershading (e.g., *Mobula* spp., rays and *Carcharhinus* spp., Sharks), possibly obscuring a distribution pattern. Background matching depends on the substrate against which the animal stands. In this way the individual can go unnoticed in one or few habitats but be quite visible in others (Endler, 1984; Duarte *et al.*, 2018), while it should also remain sedentary (Hall *et al.*, 2013). A wider habitat use may be achieved by color change, such as in *Bothus ocellatus* (Agassiz, 1831) (Ramachandran *et al.*, 1996). Furthermore, many species with homogeneous coloration are classified as nocturnal, such as batfish (Gibran, Castro, 1999), nurse sharks (Matis *et al.*, 1974), *Apogon* spp. (Livingston, 1971), *Lutjanus* spp. and *Haemulon* spp. (Hitt *et al.*, 2011). In reef there is a dramatic alternation of the diurnal fish fauna with the nocturnal fish fauna. Many of the nocturnal species spend the day in cavities in the reefs (Hobson, 1965), relying less on visual camouflage. Nevertheless, nocturnal fishes can be preyed on during the day or spotted by diurnal predators during turnover, in twilight periods (Hobson, 1979). That is why we included nocturnal species in our analysis.

Fishes with several color patterns, such as silvery, striped, spotted, or homogeneous coloration were present in the demersal stratum. This stratum is intermediate and usually has greater diversity since it receives elements from other strata around. This situation is parallel to the concept of ecotones, in which diversity is higher due to contributions from both the surrounding biomes (Risser, 1995).

The UV reflectance was not addressed in this study as we used photos from standard non-UV sensitivity cameras. However, some species may have UV reflective color patterns that may enhance or reduce the camouflage value for UV sensitive marine organisms (Losey *et al.*, 1999; Marshall *et al.*, 2015). Further, water column causes light polarization that can interfere with the camouflage of pelagic silvery fishes. Light polarization under water is usually at its maximum when looking horizontally through the water and silvering may interfere with this polarization pattern (Johnsen, 2012; Shashar *et al.*, 2000). A predator with visual sensitivity for light polarization could use this cue to find prey (Shashar *et al.*, 2000).

In our study, we categorized the images visually by a human observer. Consequently, we were limited by the human vision. Similarly, habitat categorizations and color patterns are relatively subjective, making room for divergence. Further, we restricted our analysis to Brazilian reef fishes, whose diversity is reasonably divergent from other reef ichthyofaunas (Araújo *et al.*, 2020). Nonetheless, we believe our results should be reproducible in different geographic regions because Brazilian reef fish taxonomic diversity at the family level and functional diversity satisfactorily mirror reefs in other parts of the world (Floeter, Gasparini, 2000). Including species from other regions may increase the accuracy of the analysis.

Our study is the first to correlate reef fishes color and habitat use. A search on Web

of Science on September 2021 for the terms “Fish color*” AND “Habitat use” in the topic returned 141 papers, but none specifically tested how fish color influence their water column use. In conclusion, we observed that reef fishes have color patterns that partially reflect the stratum they occupy in the water column. This is particularly clear for benthic and pelagic species, which presented predominantly disruptive patterns and silvering coloration, respectively. Therefore, this study shed light on factors that may affect color and habitat use by reef fishes. The place where a fish dwells may interact not only with its color pattern but also with how much it moves between different reef microhabitats and backgrounds.

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The authors declare no competing interests.

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